



Post-fire tree stress and growth following smoldering duff fires

J. Morgan Varner^{a,*}, Francis E. Putz^b, Joseph J. O'Brien^c, J. Kevin Hiers^d, Robert J. Mitchell^d, Doria R. Gordon^{b,e}

^a Department of Forestry and Wildland Resources, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA

^b Department of Botany, University of Florida, Gainesville, FL, USA

^c USDA Forest Service Southern Research Station, Athens, GA, USA

^d J.W. Jones Ecological Research Center, Newton, GA, USA

^e The Nature Conservancy, Gainesville, FL, USA

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ABSTRACT

Understanding the proximate causes of post-fire conifer mortality due to smoldering duff fires is essential to the restoration and management of coniferous forests throughout North America. To better understand duff fire-caused mortality, we investigated tree stress and radial growth following experimental fires in a long-unburned forest on deep sands in northern Florida, USA. We burned basal fuels surrounding 80 mature *Pinus palustris* Mill. in a randomized experiment comparing the effects of basal burning treatments on stem vascular meristems; surficial roots; root and stem combinations; and a non-smoldering control. We examined the effects of duration of lethal temperatures ($>60^{\circ}\text{C}$) on subsequent pine radial growth and root non-structural carbohydrates (starch and sugar). Duff and mineral soil temperatures in the experimental fires consistently exceeded 60°C for over an hour following ignition, with lethal temperatures of shorter duration recorded 20 cm below the mineral soil surface. Duff heating was best explained by day-of-burn Oe horizon moisture ($P = 0.01$), although little variation was explained ($R^2 = 0.24$). Post-fire changes in latewood radial increment in the year following fires was related to duration of temperatures $>60^{\circ}\text{C}$ 10 cm deep in the mineral soil ($P = 0.07$), but explained little variability in post-fire growth ($R^2 = 0.17$). In contrast, changes in non-structural carbohydrate content in coarse roots (2–5 mm diameter) 120 days following burning were more strongly correlated with the duration of lethal heating 5 cm below the mineral soil surface ($P = 0.02$; $R^2 = 0.53$). Results from this study implicate the role of mineral soil heating in the post-fire decline of mature longleaf pine following restoration fires in sandy soils.

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1. Introduction

Although frequent fires are necessary for the maintenance of many conifer-dominated ecosystems, when reintroduced after long periods of exclusion, fire can cause stress, reduce growth, and increase mortality, even among the largest trees (Swezy and Agee, 1991; Haase and Sackett, 1998; Stephens and Finney, 2002; Hood et al., 2007; Kolb et al., 2007; Varner et al., 2007). Increasing our understanding of fire-induced conifer mortality is important given current efforts to reintroduce fire to areas that have suffered long periods of fire exclusion (Covington et al., 1997; Wade et al., 1997; Agee, 2003; Varner et al., 2005). Fires reintroduced to long-unburned forests can injure root systems, stem, and canopy meristems and lead to stresses that reduce the abilities of trees to defend themselves against pathogens or weather periodic climatic

stress (Feeney et al., 1998; Kolb et al., 1998; McHugh et al., 2003). A major deficiency in our understanding of post-fire tree mortality concerns the linkages between fire behavior and its effects on tree stress and growth.

Understanding fire-induced mortality of conifers characteristically resistant to fire injury is critical to the management of fire, fuels, and forest health. While several proposed mechanisms of fire-induced mortality (i.e. injury to stem, canopy, and root meristems and second-order effects related to pathogen susceptibility) have received attention, the link between consumption of forest floor fuels and tree mortality has increasing support (Swezy and Agee, 1991; Stephens and Finney, 2002; Varner et al., 2007). For example, fire injury to surface and duff-bound roots (i.e. roots in the mor humus) was proposed as a cause of mortality in *Pinus ponderosa* Laws. (Swezy and Agee, 1991). Basal fire injury to stem vascular tissue can also cause tree stress and death (Ryan and Frandsen, 1991; Ryan, 2000). Combinations of fire-caused injuries affect tree survival, and several investigators report the strongest correlates of post-fire mortality are those that include injuries to

* Corresponding author. Tel.: +1 707 826 5622; fax: +1 707 826 5634.

E-mail address: jmvarner@humboldt.edu (J. Morgan Varner).

multiple tissues (Ryan and Reinhardt, 1988; Ryan et al., 1988; Saveland and Neuenschwander, 1990; Ryan, 2000; Stephens and Finney, 2002; Varner et al., 2007). Distinguishing the actual causes of mortality will help managers modify their actions to avoid or minimize post-fire tree mortality. Second-order fire effects such as bark beetle infestations (Dixon et al., 1984; Menges and Deyrup, 2001; McHugh et al., 2003) and fungal infections (Ostrosina et al., 1997; Ostrosina et al., 1999) are cited as causes of post-fire decline and mortality, but are likely linked to compromises in tree defenses caused by antecedent fire-caused injury to stem, crown, or root tissues. The inability to establish a relationship among the responses of trees, the characteristics of the fire (i.e. temperatures and duration of lethal heating to a temperature $>60^{\circ}\text{C}$; Byram, 1958), and the fuels that fed them inhibits restoration of fire-excluded ecosystems.

Post-fire tree mortality has been a difficult topic of inquiry, particularly given the complications of working with the diversity of individual fires and the multifaceted interactions between injured trees and stresses caused by insects, diseases, climatic variation, and competition from other trees (Franklin et al., 1987). One approach to overcoming the complications of post-fire mortality research is the investigation of the effects of a diversity of fires (with heating concentrated or segregated to focal tissues) on the precursors of tree death: stress (Manion, 1981; Waring, 1987) and reduced growth (Pedersen, 1998; van Mantgem et al., 2003). Post-fire water stress was proposed by Ryan (2000) as a cause of post-fire decline in *P. ponderosa*. Ryan found that stem injury caused by basal heating led to reduced transpiration and conductance, although the response was delayed and followed a short-term increase in both factors. In *Pinus halepensis* Mill., Ducrey et al. (1996) found stomatal conductance to decrease within one week of basal fires. In longleaf pine (*Pinus palustris* Mill.), O'Brien et al. (2009) found the same rapid water stress phenomenon to occur, but their results were tightly linked to consumption of basal duff, incorporating the potential effects of root heating on mortality. Post-fire growth losses have been observed in many species, often as a precursor to eventual death (e.g., Johansen and Wade, 1987; Ducrey et al., 1996; Busse et al., 2000; van Mantgem et al., 2003). Stress and growth also offer investigators the ability to detect continuous effects of injury, rather than the binary (either "alive" or "dead") response that mortality research utilizes; this point reveals the potential for minor alterations in fire management that generate marked changes in reducing tree stress or minimizing post-fire growth loss. What is needed is generation of a more sound understanding of fire-caused stress, its effects on tree growth, and the linkages to tree mortality. Longleaf pine, a species with widely acknowledged resistance to fire injury across its life history, is a species that natural resource managers have substantial interest in restoring fire to while minimizing post-fire mortality (Varner et al., 2005).

The objectives of this study were to link fuels, specific types of basal injury to individual trees, and fire behavior to the subsequent growth, stress, and mortality of mature longleaf pine in replicated small-scale burns. We selected root non-structural carbohydrates to estimate tree stress in fine and coarse roots (Wargo et al., 1972; Marshall and Waring, 1985; Kozłowski and Pallardy, 1997). Radial stemwood growth was used to assess effects on tree growth (Busse et al., 2000). Specifically, we tested the following hypotheses: (i) first-year post-fire radial growth would decrease with increasing duration of lethal heating (temperatures $>60^{\circ}\text{C}$) to stem and soil and these changes would be exacerbated in latewood growth, (ii) following fire, coarse root (2–5 mm diameter) non-structural carbohydrates would decrease with increasing duration of lethal heating to basal bark and roots in duff and mineral soil, and (iii) tree mortality would increase with greater durations of duff smoldering. This work was designed to inform regional restoration

efforts and contribute to our understanding of the larger issue of post-fire overstory tree decline and mortality increasingly common in many North American coniferous ecosystems.

2. Methods

2.1. Study site

This experiment was conducted in a long-unburned (37 years since fire) longleaf pine stand at the Ordway-Swisher Biological Station near Melrose (Putnam County), Florida, USA ($\text{N}29^{\circ}40'$, $\text{W}81^{\circ}74'$). The stand was dominated by an overstory of longleaf pine, with a dense midstory of oaks (*Quercus laevis* Walt., *Q. geminata* Small, and *Q. hemisphaerica* Bartr.), a patchy remnant groundcover dominated by *Aristida stricta* Michx., and a thick organic forest floor (depths to 15 cm) typical of long-unburned xeric southeastern pine ecosystems (Varner et al., 2005). Soils of the site are deep, excessively well-drained hyperthermic, uncoated Lamellic Quartzipsamments in the Candler series (Readle, 1990). The topography is gentle, with north-facing slopes $<5\%$ and elevations averaging 36 m above msl. The climate is humid, warm temperate with long, warm, and humid summers and short, mild winters with annual temperatures and precipitation averaging 20°C and 1432 mm, respectively (Readle, 1990).

2.2. Experimental design

Eighty mature (30–50 cm diameter at breast height) individual longleaf pines across a 2 ha area were randomly selected as experimental units for examination of fire-induced stress, growth, and mortality. Four treatments (20 replicates per treatment) were assigned to trees in a completely randomized design. The treatments allowed comparison of three hypothesized causes of post-fire mortality: (1) root and stem injury (ROOT + STEM), (2) root injury (ROOT), and (3) stem injury (STEM). A control treatment was installed for comparison where trees were burned but smoldering phase combustion was extinguished (CONTROL). Individual pines formed the center of 1 m radius circular plots in which measurements were focused (Fig. 1). Each tree was ring-ignited with a drip torch from a raked line 1 m from the tree base. In the ROOT + STEM treatment, fires were allowed to consume the forest floor without protection, thereby heating both basal bark and underlying roots (Fig. 1). ROOT treatments were accomplished by moving accumulated basal forest floor fuels 5–10 cm away from the stem, a sufficient distance to prevent basal bark heating while minimally disturbing basal fuels. In the STEM treatments, basal bark was heated by burning a 20 cm radius area surrounding each tree base; the adjacent forest floor (and underlying roots) was protected with 10 cm tall aluminum flashing sheathed in fire shelter material (Cleveland Laminating Corp., Cleveland, OH, USA) and its base buried approximately 2 cm in surface mineral soil to prevent escapes. CONTROL burns were carefully extinguished with a 30 cm \times 30 cm flapper once flaming combustion ended and watered if O horizon smoldering persisted. Experimental fires spanned a 34-day period beginning 25 September and concluding 4 November 2003.

2.3. Tree measurements

Post-fire tree changes in growth were assessed using stem radial growth following burns (Busse et al., 2000). Radial stem growth (mm) of all 80 burned treatment trees was measured using 5 cm deep increment cores (2 per tree, 90° apart) extracted 1-year post-burn (January–February 2005) at 1 m above the ground. Cores were air-dried, mounted, and sanded according to standard dendrochronological methodology (Stokes and Smiley, 1968). All

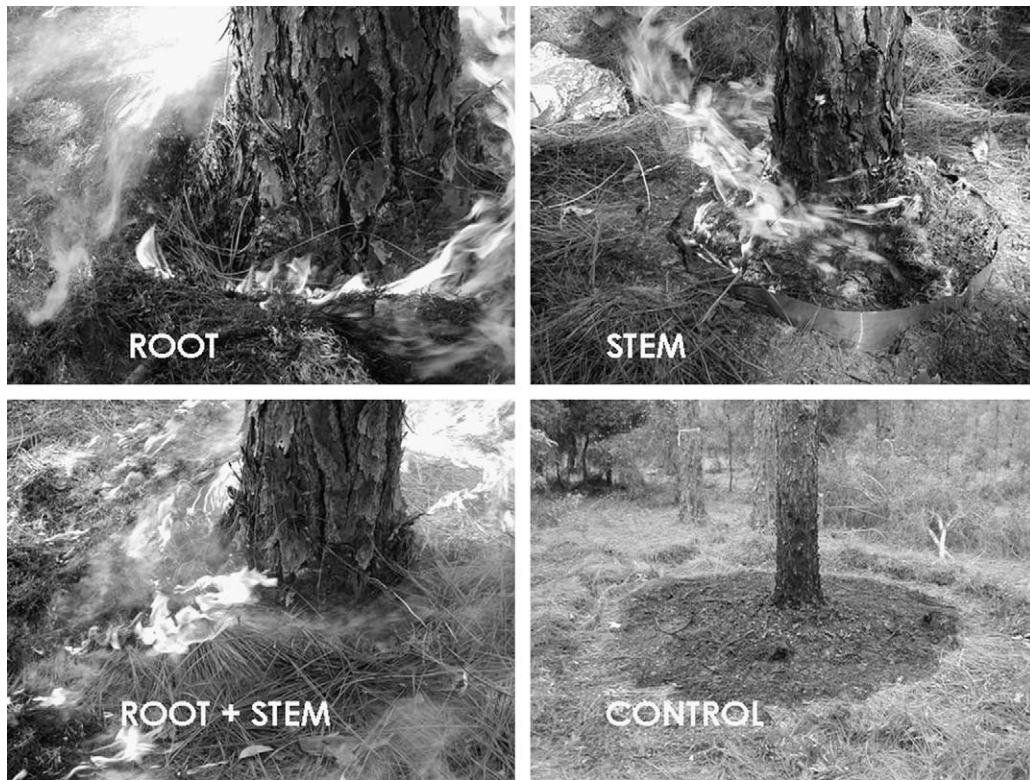


Fig. 1. Experimental fire treatments to individual pines in a long-unburned *Pinus palustris* forest in northern Florida, USA. The treatments were, clockwise from top left: ROOT, ROOT + STEM, STEM, and CONTROL. Treatments were designed to isolate heating to target tissues (i.e., ROOT treatments were designed to heat only root tissues, while STEM treatments were designed to isolate heating on stem tissues).

cores were measured using a binocular microscope with 2003 and 2004 earlywood and latewood measured to the nearest 0.01 mm.

Tree stress following burns was estimated using changes in non-structural carbohydrate concentrations (starch + sugar) in fine and coarse roots (Wargo et al., 1972; Marshall and Waring, 1985; Kozłowski and Pallardy, 1997). Within a randomly selected subset of 8 trees in each treatment ($n = 32$), total non-structural carbohydrate concentrations in roots were sampled within 10 days and again at 4 months post-burn (hereafter, “tnc₁₀” and “tnc₁₂₀”). The tnc₁₀ trees were sampled within 3–10 days post-fire to minimize transformations of carbohydrates from their pre-treatment pools (Kozłowski and Pallardy, 1997). For each root carbohydrate sample, 3 g (dry weight) of fine (1–2 mm diameter) and 3 g of coarse (2–5 mm diameter) longleaf pine roots were unearthed from the upper 20 cm of mineral soil within a 50 cm radius surrounding treatment trees until a sufficient mass was gathered (typically a small, approximately 25 cm × 25 cm ground area was disturbed). All roots were bagged and immediately stored on dry ice in a cooler. Immediately upon removal from chilling, the roots were rinsed and oven-dried at 100 °C for 2 h, followed by drying at 70 °C to a constant mass to minimize post-harvest carbohydrate losses (Smith, 1969).

Root non-structural carbohydrate samples were analyzed using a modified phenol-sulphuric acid method (Buysse and Merckx, 1993). From each fine and coarse root sample, 80 mg were extracted for 12 h in 10 ml 80% ethanol then centrifuged at 2200 rpm for 15 min. The resulting supernatant was removed and placed in a 50 ml flask. The residue was centrifuged a second time in 5 ml 80% ethanol for 5 min, and the supernatant was transferred to the same volumetric flask. The residue from the ethanol extractions was transferred to a glass tube, dried, and then boiled for 3 h in a 5 ml 3% HCl. The filtrate was adjusted to 50 ml in a

volumetric flask and used for the starch analysis. For total sugar and starch determinations, 1 ml of a solution containing 20 to 80 µg sugar was transferred into a glass tube and 1 ml of a 28% phenol in 80% ethanol was added. Five ml of concentrated sulfuric acid was immediately added directly to the liquid surface. The tube was agitated for 1 min and allowed to stand for 15 min prior to measuring absorbance at 490 nm in a Shimadzu UV spectrophotometer (Shimadzu Corporation, Kyoto, Japan).

Pines from all 4 treatments ($n = 80$) were surveyed for mortality at 4, 8, 12, and 24 months after the burns to capture the pattern of delayed mortality across and within treatments. Since burning treatments were focused on the bases, no crown scorch occurred during any fire.

2.4. Forest floor at tree bases

To understand the effects of fuels on fire intensity and subsequent tree injury, we intensively characterized forest floor accumulations surrounding treatment pines. We measured forest floor depth and consumption surrounding each burned tree using eight 20 cm tall steel pins installed flush with the top of the forest floor 8 cm from the stem in cardinal and ordinal directions. Following all burns, pins were measured for forest floor depth reduction (cm exposed on pins) and averaged for each plot. To estimate forest floor fuel moisture contents, forest floor fuels (Oi, Oe, and Oa horizons collected separately) and pine cones (3 recently fallen, 3 decomposing) were collected within 20 min of ignition on each burn day from unburned trees proximal to treatment trees (Table 1). Pine cones were collected since they serve as vectors of duff ignition (Fonda and Varner, 2005). In the laboratory, fuels were weighed before and after drying at 70 °C to a constant weight to determine day-of-burn fuel moisture content and dry mass.

Table 1

Fire weather observations and time-of-ignition fuel moistures from 80 experimental single-tree burns at the Ordway-Swisher Biological Station, Florida, USA. All experimental fires burned between 25 September and 4 November 2003.

Weather variable	Mean \pm s.d.	Maximum	Minimum
Air temperature ($^{\circ}$ C)	27.8 \pm 2.37	32.0	25.3
Relative humidity (%)	58.3 \pm 6.19	67.0	51.0
2-m wind speed (m s^{-1})	0.9 \pm 0.41	1.3	0.4
Oi horizon moisture (%)	14.9 \pm 3.4	19.1	9.4
Oe horizon moisture (%)	64.5 \pm 59.9	186.3	11.6
Oa horizon moisture (%)	55.9 \pm 23.3	100.4	36.2
Pine cone moisture (%)	21.0 \pm 18.4	47.7	6.5
A horizon (0–20 cm) moisture (%)	7.1 \pm 3.1	12.7	3.8

2.5. Fire measurements

Fire temperatures were measured on a subset of all treatment trees (6 trees per burning treatment, $n = 24$) during fires using Type J thermocouples (range 0–1200 $^{\circ}$ C; Omega Laboratories, Stamford, CT, USA) connected to a Campbell Scientific CR10X datalogger (Campbell Scientific, Logan, UT, USA). Temperatures were measured on the basal bark surface at three points 120 $^{\circ}$ apart at approximately 10 cm above the mineral soil surface (near the forest floor–bark interface; Fig. 2). To estimate root and soil heating, thermocouples were buried 120 $^{\circ}$ apart in the lower duff (Oa horizon) approximately 10 cm from the tree base, and directly beneath these points in the mineral soil at 5, 10, and 20 cm depths (Fig. 2). To minimize soil disturbance, thermocouples were inserted into the soil in narrow openings created by slicing into the soil at a slight angle with a machete and then inserting the thermocouple lead at the predetermined depth. Maximum and mean temperatures were stored every 2 min from 15 min pre-ignition to 1700 h when the fires were required to be extinguished according to prescription and burn permits from the Florida Division of Forestry. While truncated, this artificial burn extinction was applied equally to all treatments and also fits with regional land management practices (Wade and Lunsford, 1989).

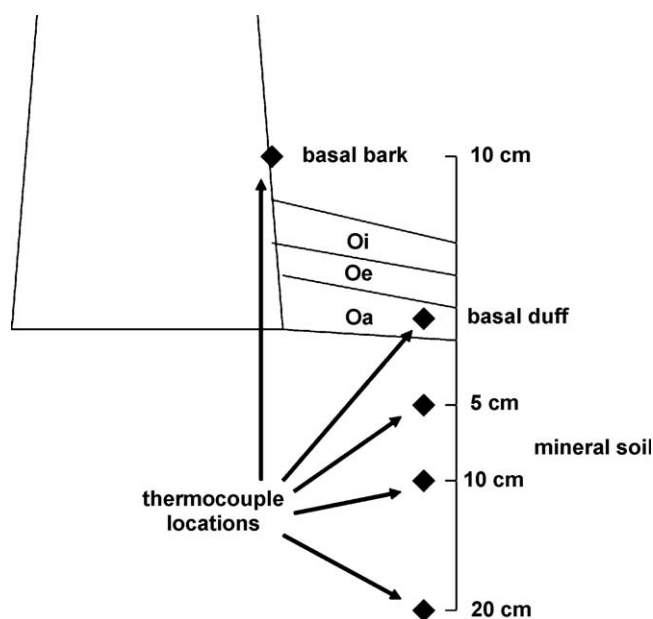


Fig. 2. Locations of thermocouples during experimental fires surrounding the base of an individual long-unburned *Pinus palustris* tree. At each measured tree ($n = 8$ per treatment), thermocouples were attached at three locations 120 $^{\circ}$ apart in each strata: on the basal bark, inserted into lower duff (Oa horizon), and inserted at depths of 5, 10, and 20 cm in the mineral soil. Thermocouples measured temperatures from 15 min prior to ignition until the fires were extinguished at 1700 h.

Fire behavior, weather, and fuel consumption were recorded for each experimental fire. Fire measurements included maximum flame length (cm; ocularly estimated), flaming time (sec; stopwatch), and residual smoldering time (s; stopwatch). Fire weather (2 m wind speed, air temperature, and relative humidity) was recorded periodically during all experimental fires (Table 1). Post-burn forest floor consumption was estimated by measuring the difference in pin exposure following fires.

2.6. Data analysis

The experiment was a completely randomized design with 4 treatments (ROOT, STEM, ROOT + STEM, CONTROL) with 20 replicates in each treatment. ANOVA was used to detect overall treatment effects, with any pair-wise differences among treatments determined using a post hoc Tukey–Kramer HSD test ($\alpha = 0.05$). The effects of treatments were tested on forest floor consumption (cm), duration (min) of heating >60 $^{\circ}$ C (an approximation of lethal temperature for plants; Byram, 1958), changes in 1-year post-burn radial growth (earlywood and latewood increment; %), mortality 24-month post-burn (%), and short-term (120 days) post-burn changes in root non-structural carbohydrates (fine and coarse roots; %). To examine relationships between fuel moisture contents (Oi, Oe, Oa, cones, 0–5 cm mineral soil) as predictors of fire behavior response variables (flame length, flaming duration, smoldering duration), we used step-wise regressions. Step-wise regression was also used to relate heating duration in the different strata (bark, duff, and mineral soil) to 24-month post-fire tree mortality (%), 1-year radial growth (% change in earlywood and latewood increment, 2003–2004), and changes in root non-structural carbohydrates (fine and coarse roots, $\text{tnc}_{10} - \text{tnc}_{120}$) post-burn response variables. To meet assumptions of parametric analyses, any non-normal data were transformed prior to analysis according to convention (Zar, 1996). Finally, given the correlations among strata (i.e. the burning of duff fuel provides heat to underlying mineral soil horizons that subsequently heat lower horizons), all regression model iterations were evaluated for potential multicollinearity (Hintze, 2007).

3. Results

3.1. Fire behavior

Flame lengths during the experimental burns ranged from 0.4 to 3.0 m (mean = 1.52 m; s.d. = 0.70 m, $n = 80$), did not vary among treatments, and were within the range of large restoration fires in the region. Fire temperatures on the instrumented trees ($n = 24$) during experimental burns were highest above-ground, with average maximum basal bark temperatures in individual fires ranging up to 476 $^{\circ}$ C, average maximum duff temperatures up to 304 $^{\circ}$ C, and average maximum mineral soil temperatures at 5, 10, and 20 cm below the surface to 134, 117, and 80 $^{\circ}$ C, respectively. Lethal heating durations were longest in duff (mean = 74 \pm 168.8 min), next longest on basal bark (mean = 36 \pm 73.9 min), and in the mineral soil decreased with depth (27 \pm 4.8, 7 \pm 14.4, 1 \pm 2.5 min at 5, 10, and 20 cm depths, respectively; Table 2). Following ignition, basal bark temperatures increased first, then duff, followed by sequential depths in the mineral soil. After initial heating, basal bark temperatures across all treatments dropped below 60 $^{\circ}$ C. As intended, basal bark temperatures were higher in ROOT + STEM and STEM treatments than in ROOT and CONTROL treatments ($P = 0.06$, $\text{df} = 3$, $F = 2.91$; Table 2). Using the Peterson and Ryan (1986) cambial mortality model, we estimate that the duration of basal bark surface temperatures observed here caused little underlying cambial cell mortality; only three instrumented trees weathered lethal temperatures on their bark for more than 50 min. Duff and mineral

Table 2

Durations of lethal heating (i.e. temperatures $>60^{\circ}\text{C}$) to basal bark, duff, and mineral soil during individual tree burns at the Ordway-Swisher Biological Station in northern Florida, USA.

Treatment ^a	Duration of temperatures $>60^{\circ}\text{C}$ (min)				
	Basal bark	Basal duff	5 cm soil	10 cm soil	20 cm soil
STEM ($n=6$)	44.3 \pm 77.1	42.9 \pm 47.3	7.9 \pm 14.1	7.3 \pm 17.9	–
ROOT ($n=6$)	10.1 \pm 7.0	145.6 \pm 283.7	41.0 \pm 90.5	4.6 \pm 9.9	0.7 \pm 0.8
ROOT + STEM ($n=6$)	82.2 \pm 121.8	95.7 \pm 187.3	56.1 \pm 122.2	12.8 \pm 20.9	2.1 \pm 4.8
CONTROL ($n=6$)	9.4 \pm 2.6	10.6 \pm 24.6	2.7 \pm 5.9	1.4 \pm 3.5	0.2 \pm 0.5
Means	36.5 \pm 73.9	73.7 \pm 168.8	26.9 \pm 74.8	6.5 \pm 14.4	0.8 \pm 2.5

^a Treatments were intended to isolate long-duration heating to either roots (ROOT), basal stems (STEM), both roots and stem tissues (ROOT + STEM), or surface fuels burned with no long-term smoldering (CONTROL).

Table 3

Effects of individual tree experimental burning treatments on smoldering time, mean floor consumption, longleaf pine stem radial growth, and root non-structural carbohydrates in northern Florida, USA.

	Burning treatment				N	P
	ROOT	ROOT + STEM	STEM	CONTROL		
Smoldering time (min)	6.9 \pm 6.7 A	8.9 \pm 8.6 A	6.8 \pm 6.8 A	1.1 \pm 2.2 B	8	0.018
Forest floor consumption (cm)	6.3 \pm 1.8 AB	9.1 \pm 3.1 A	7.0 \pm 3.0 AB	4.6 \pm 2.0 B	8	<0.001
Radial growth (% change 2003–2004)	–17 \pm 19	–19 \pm 36	–28 \pm 33	–22 \pm 19	8	0.582
Fine root carbohydrates (% change 2003–2004)	6.3 \pm 16.6	12.6 \pm 14.3	–9.3 \pm 16.5	8.1 \pm 26.3	8	0.246
Coarse root carbohydrates (% change 2003–2004)	–5.6 \pm 27.1	–12.8 \pm 46.8	–3.3 \pm 44.1	9.9 \pm 16.2	8	0.584

^a Values within rows followed by a different letter indicate significant differences among treatments, determined using a post hoc Tukey–Kramer HSD with $\alpha=0.05$ prior to analysis.

Table 4

Regression results for the analysis of fuel and soil moisture effects on basal bark, duff, and mineral soil temperatures in smoldering fires in a long-unburned longleaf pine stand in northern Florida, USA.

Dependent variables	β_0	β_1	R^2	P
\log (basal bark temperatures $>60^{\circ}\text{C}$; min)	3.86	–0.019 (% Oa moisture)	0.16	0.053
\log (duff temperatures $>60^{\circ}\text{C}$; min)	3.61	–0.018 (% Oe moisture)	0.24	0.015
5 cm mineral soil temperatures $>60^{\circ}\text{C}$ (min)				NS ^a
10 cm mineral soil temperatures $>60^{\circ}\text{C}$ (min)				NS
20 cm mineral soil temperatures $>60^{\circ}\text{C}$ (min)				NS

^a Dependent variables with “NS” and no listed independent variables were not significantly related to any of the measured predictor variables.

soil temperatures at all depths, in contrast, were highly variable and did not differ among treatments (Table 2). Average forest floor consumption at the base of pines differed among treatments ($P < 0.001$, $df = 3$, $F = 6.69$; Table 3), ranging from a low of 4.6 cm reduced in the CONTROL to a high of 9.1 cm reduced in the ROOT + STEM treatment. Smoldering time also differed among burning treatments ($P = 0.018$, $df = 3$, $F = 5.49$; Table 3), with all smoldering treatments (ROOT, ROOT + STEM, and STEM) burning 6–8 min longer than the CONTROL treatment.

Temperatures on the basal bark and within the duff, and at 5, 10, and 20 cm deep in the mineral soil were related to day-of-burn duff moisture parameters. In a step-wise regression with day-of-burn fuel moistures and weather observations as independent variables, the duration (min) of basal bark temperatures $>60^{\circ}\text{C}$ was best predicted by lower duff (Oa horizon) moisture content ($P = 0.05$, $R^2 = 0.16$; Table 4). The best

step-wise fit for duration of duff temperatures $>60^{\circ}\text{C}$ was a univariate function of Oe moisture (fermentation horizon or “upper duff”) moisture content ($P = 0.01$, $R^2 = 0.24$). No fuel moisture predictors (including mineral soil moisture) were related to heating duration in the underlying mineral soil (5, 10, and 20 cm depths; Table 4).

3.2. Radial growth and mortality

Neither earlywood nor latewood growth differed among treatments. In a regression with thermocoupled trees as replicates ($n = 32$), earlywood increment (% change from 2003 radius) was apparently insensitive to heating durations, but the regression marginally related latewood growth to duration of mineral soil temperatures $>60^{\circ}\text{C}$ at 10 cm deep in the mineral soil ($P = 0.07$, $R^2 = 0.17$; Table 5). In the first year following fires no trees died in

Table 5

Effects of basal bark, duff, and mineral soil temperatures on longleaf pine stem radial growth and root non-structural carbohydrates following individual tree fires in northern Florida, USA. Results are based on step-wise linear regressions with minutes of basal heating $>60^{\circ}\text{C}$, duff heating $>60^{\circ}\text{C}$, 5 cm mineral soil $>60^{\circ}\text{C}$, 10 cm mineral soil $>60^{\circ}\text{C}$, and 20 cm mineral soil $>60^{\circ}\text{C}$ as potential predictor variables.

Dependent variable	β_0	β_1	R^2	P
Radial growth (% change 2003–2004)	–0.22	0.045 \log (5 cm min $>60^{\circ}\text{C}$)	0.16	0.08
Earlywood growth (% change 2003–2004)				NS ^a
Latewood growth (% change 2003–2004)	21.7	–19.4 \log (10 cm min $>60^{\circ}\text{C}$)	0.17	0.07
Fine root carbohydrates (% change 2003–2004)				NS
Coarse root carbohydrates (% change 2003–2004)	7.1	–36.7 \log (5 cm min $>60^{\circ}\text{C}$)	0.53	0.02

^a Dependent variables with “NS” and no listed independent variables were not significantly related to any of the measured predictor variables.

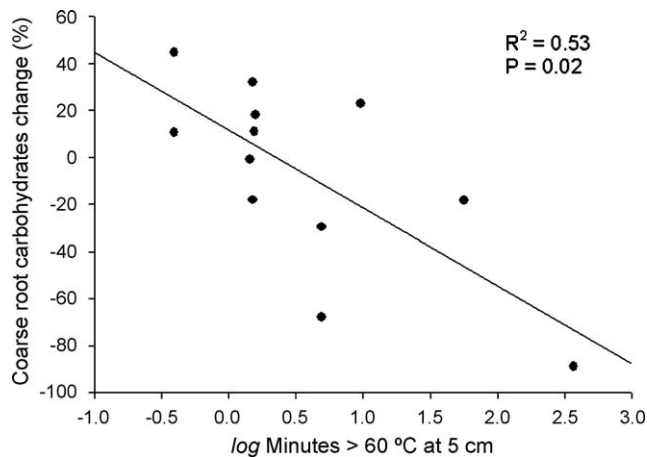


Fig. 3. Relationship between the change (2003–2004) in coarse root non-structural carbohydrates (sugar + starch) in mature *Pinus palustris* and duration of lethal heating (temperatures $>60^{\circ}\text{C}$) at 5 cm below the surface of the mineral soil in experimental fires in northern Florida, USA.

any treatment, and only one tree died in the first 24 months (a single ROOT + STEM tree).

3.3. Root non-structural carbohydrates

As with radial growth, changes in root non-structural carbohydrates did not vary among the burning treatments (Table 3). There were patterns in carbohydrate responses, however, when trees from all burning treatments were combined as replicates. While fine root carbohydrates were insensitive to lethal heating durations, coarse pine root carbohydrate stocks decreased precipitously with greater burning duration (Table 5). Lethal heating duration at 5 cm depths in the mineral soil significantly reduced coarse root carbohydrates ($P < 0.02$), explaining 53% of the variation in post-burn changes in coarse root carbohydrates (Fig. 3).

4. Discussion

Fire effects research suffers from a poor understanding of mechanistic linkages between fire injury and post-fire stress and decline (Swezy and Agee, 1991; Ryan, 2000; Dickinson and Johnson, 2001). In this study, post-fire stress, as indicated by reductions in coarse root carbohydrates, was linked to the duration of mineral soil heating caused by overlying smoldering duff in these sandy soils. Additionally, post-burn radial latewood growth rates during the first year following the fires declined with greater duration of lethal heating in the upper 10 cm of mineral soil (Table 5). These results suggest that injury from mineral soil heating decreases radial growth following fire, lending some support for a soil heating mechanism for post-fire tree decline. Changes in coarse root carbohydrates found in this study provide more strength to the role of mineral soil heating as a primary cause of post-fire tree stress. Whereas stem radial growth in longleaf pine represents an aggregate result of both the current and preceding year's conditions (Meldahl et al., 1999), carbohydrate supplies are metrics of current tree stress (Wargo et al., 1972; Marshall and Waring, 1985; Dunn and Lorio, 1992; Kozłowski and Pallardy, 1997; Guo et al., 2004). Long-duration lethal heating in the mineral soil at 5 cm depths explained 53% of the variation in post-burn losses in coarse root carbohydrates, providing substantial support for mineral soil heating as a cause of overstory tree stress. While little mortality was observed in this study, our results of decreased growth and root carbohydrate drain may be linked to the

widespread tree mortality reported following restoration fires region-wide (Wade et al., 1997; Varner et al., 2005, 2007).

As has been reported in several other studies of fire effects on North American conifers (e.g., Ryan, 2000; Stephens and Finney, 2002; Agee, 2003; McHugh and Kolb, 2003; Varner et al., 2005), there was little mortality within the first 2 years following fires. The reason for such low mortality may be the truncated duration of the experimental fires or the climate following the fires. In contrast to the preceding years, the first post-fire year (2004) was the wettest year in the previous decade and terminated the longest sustained drought in northern Florida in 50 years (NCDC, 2005), potentially concealing or delaying the effects of injury or short-term stress. Both Ryan (2000) in ponderosa pine and Sword Sayer and Haywood (2006) in longleaf pine, found that root carbohydrate response interacted with climate, where drought resulted in reduced root starch storage.

None of the experimental fire treatments (ROOT, ROOT + STEM, STEM, or CONTROL) differed in radial stem growth, root carbohydrate drain, or tree mortality (Table 3). Durations of lethal temperatures across all treatments varied, but lethal heating durations generally followed the expected pattern: CONTROL durations of heating $>60^{\circ}\text{C}$ in all strata (bark, duff, 5, 10, and 20 cm depths) were the shortest; STEM durations $>60^{\circ}\text{C}$ were low below-ground; ROOT durations $>60^{\circ}\text{C}$ were lowest on the bark; and ROOT + STEM durations were consistently longer across all strata. Mortality was surveyed periodically for 24 months, with no apparent treatment-induced mortality. Although the level thought to achieve lethal heating was obtained, only one tree died over the 24-month post-fire survey. Future research should seek to segregate heating more vigorously, perhaps with the use of fire simulator devices to focus heating (Greene et al., 1986) and more elaborate heat exclusion materials (to exclude heat from non-target tissues) and sustain injury across a wider spectrum of heating durations.

Regardless of mechanism (root or basal meristem injury), one major shortcoming in our understanding of smoldering fires is linking the fuel (basal duff) to tree injury. Basal duff is compositionally and structurally complex, hence the determinants of its ignition, smoldering duration, and extinguishment are poorly understood (Miyanishi and Johnson, 2002). In this study, the best predictive model explained only 16–24% of the variation in duration of duff temperatures $>60^{\circ}\text{C}$ and none of the measured factors explained durations of mineral soil heating (Table 4). Given the importance of duff smoldering and its implications for conifer mortality throughout North America, future work should focus on better characterizing duff fuels, the variation in duff moisture content, and determinants of duff ignition and combustion. With continued large-scale fire exclusion in southeastern pine forests and in coniferous forests elsewhere in North America, problems with duff smoldering will continue.

Among the most striking results of this experiment was the depth and duration of heating in the lower duff and surface mineral soil (Table 2). In the ROOT and ROOT + STEM treatments, mineral soil temperatures were elevated substantially above ambient (21°C) to 20 cm below the mineral soil surface for long durations. This finding seems important given that in long-unburned longleaf pine stands targeted for restoration, most fine roots grow within basal duff and the upper few centimeters of mineral soil (Heyward, 1933; O'Brien et al., 2009). Mineral soil heating, the most prominent predictor of reductions in growth and stored carbohydrates, exceeded 60°C in the top 5 cm in 58% of all burns (75% of treatments designed for root-only heating), as well as at lower depths: 42% and 25% of all burns had temperatures $>60^{\circ}\text{C}$ at depths of 10 and 20 cm below the surface, respectively. Data from an extended overnight burn (4 November 2003; only temperature data prior to 1700 were

included in the analyses) revealed temperatures in the mineral soil can exceed lethal values for >19 h (these burns were extinguished at 0900 h the following day, when all were still smoldering), perhaps indicative of how other trees would have burned if not extinguished and how fuels smolder in large landscape fires. Managers and other reports in the region (Wade et al., 1997) note smoldering lasting for days post-ignition if not extinguished. Our substantial below-ground heating results may be more exaggerated in the deep sandy soils found in our study site; research across soil texture gradients may unearth different patterns of soil and root heating.

Duff and soil heating, even with the artificially truncated durations in this study, provide support for fire-caused root injury in smoldering fires (Swezy and Agee, 1991). Prolonged heating kills small pine roots, but also injures or kills higher-order roots (as in Guo et al., 2004) that connect large numbers of smaller roots to the tree, cascading localized effects into more substantial whole-tree injury. Following 2003 landscape restoration fires in northwestern Florida, two of the authors (JMV and RJM) observed several large pines with recently killed main-channel roots. If allowed to smolder without artificial extinguishing, trees in this study may have suffered even greater below-ground injury. Given the observed link between the duration of lethal heating in the soil and carbohydrate drain, it appears that prolonged smoldering exacerbates post-fire stress and may lead to tree death. Soil heating can kill fine roots, which then creates a demand for carbohydrates for their replacement. Soil heating may not be the sole cause of tree decline and mortality, but the links among duration of lethal temperatures, reduced stem radial growth, and root carbohydrate drain underscore our need to understand fire injury and the physiological response to fire-caused insults (Ducrey et al., 1996; Ryan, 2000; Dickinson and Johnson, 2001).

Although we did not observe substantial post-fire mortality in this study, our findings suggest a mechanism for post-fire tree decline observed in longleaf pine and other conifers. Coarse root carbohydrate concentrations in this study were reduced drastically by smoldering-induced heating of mineral soil (Fig. 3) whereas fine root carbohydrate concentrations were unaffected by heating duration. This pattern (carbohydrate drain in coarse roots while fine root carbohydrate pools remain unchanged) in concert with findings from landscape fires (Varner et al., 2007) where duff consumption was strongly linked to tree mortality are provocative. These findings support a model of post-fire stress where injured trees use available carbohydrate storage to replenish killed or injured fine roots, depleting carbohydrate reserves and thereby compromising the tree. If stressed further, these fire-weakened trees then could succumb to second-order pests, diseases, or climatic stress, all of which have been suggested as causes of death in regional restoration fires (Ostrosina et al., 1997, 1999; Menges and Deyrup, 2001; Sword Sayer and Haywood, 2006). Evidence here and in other studies support the strong need for finer scale attempts at reconciling tree stress, growth, and death in response to smoldering fires.

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